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Article

Habitat structure and its influence on populations of *Amblydromalus limonicus* (Acari: Phytoseiidae)

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Abstract

Cannibalistic behaviour can be a limitation in mass rearing where predator-predator competition can be high. However, increasing habitat structural complexity has been shown to reduce cannibalism through a reduction in encounter rates and the provision of more refuge and oviposition sites. This study investigated the use of different rearing media and its ability to mitigate cannibalism in the predatory mite *Amblydromalus limonicus* (Garman & McGregor). The rearing substrates tested were buckwheat husks, gorse husks, rice husks, vermiculite, and wheat bran, which were compared against a control treatment with no substrate. These laboratory experiments were done in two different relative humidities (70% and 85%) with both water and pollen (*Typha orientalis* Presl) supplementation. The rearing media had a strong significant effect on populations of *A. limonicus* while humidity did not. Rice husk was found to hold the highest populations of the predator, whereas the control and wheat bran treatments had the lowest. The higher populations associated with the rice husk treatment were attributed to a decrease in encounter rates, the provision of additional shelter and oviposition sites, and low mould infestation. Issues with sampling bias, effects of mould in the system, and potential applications of rice husk are discussed.

Key words: *Amblydromalus limonicus*, habitat structure, rearing media, mass rearing, biocontrol

Introduction

Cannibalism among predatory mites of the family Phytoseiidae is prevalent and has been documented for decades (Momen & Abdel-Khalek 2009; Schausberger 1997, 2003; Walzer & Schausberger 1999a; Zhang & Croft 1995). Due to the importance of predatory mites in controlling key pests in agricultural systems, there has been much interest in their cannibalistic behaviour. Although cannibalism may reduce population density, it may serve to enhance population longevity after prey elimination (Rasmy & Saber 2012; Schausberger 2003; Schausberger & Croft 2000). Other suggested benefits of cannibalism by predatory mites are the absorption of nutrients when prey density is low, decrease of intraspecific competition for food and physical resources such as oviposition sites, and lastly the elimination of a potential predator (Croft *et al.* 1995; Schausberger 2003; Schausberger & Croft 2000). These are balanced by the costs of the behaviour which include the risk associated with attacking the prey itself, risk of transmission of host-specific diseases and parasites, and the potential of killing a kin and thus reducing genetic fitness (Pfennig 1992; Schausberger 2003). Factors such as nutritional benefits, the role of life stage, and species and kin discrimination have been investigated in order to further understand the process of cannibalism (Croft *et al*. 1996; Faraji *et al.* 2000; Schausberger 2003; Schausberger & Croft, 2000).

The Phytoseiidae family has become one of the archetypes of cannibalistic behaviour at the individual level (Schausberger 2003). Mechanisms behind cannibalism are crucial to the understanding of their behavioural ecology as it can significantly alter population structure and dynamics within a habitat (McCann *et al*. 1998). This in turn affects the applicability of a cannibalistic species for mass rearing and hence biological control operations as a whole. Predatory mites such as *Amblydromalus limonicus* (Garman & McGregor), have a huge potential in the control of greenhouse pests due to its wide prey range (Knapp *et al*. 2013). *A. limonicus* has been classified as a type III generalist predator that feeds on several types of prey including thrips, psyllids, whiteflies, and tetranychid mites (Davidson *et al*. 2016; McMurtry *et al*. 2013; Xu & Zhang 2015). This species can also utilise pollen, honeydew, various plant exudates, and even plant tissue as a food source (McMurtry 1992; Messelink *et al*. 2006; Nguyen *et al*. 2015; Vangansbeke *et al*. 2014b). Like most phytoseiids, *A. limonicus* also displays cannibalistic behaviour. Cannibalism in phytoseiids can act as a barrier in optimising mass rearing operations. This behaviour may also cause negative flow on effects in the greenhouse environment when populations begin to increase exponentially (Hardman *et al*. 2013; Lesna *et al*. 2014). This would thus create competitive conditions for the predatory mites which would likely lead to an increase in cannibalism and thus a decrease in population density.

The main goal of mass rearing practices is to achieve high densities of a particular biological control agent (Sørensen *et al*. 2012). When high densities are attained, populations become limited by the food and space available, thereby negatively impacting on the biology of the control agent (Allawi 1991; Kuriwada *et al.* 2009). Furthermore, this high density may promote cannibalism of eggs and vulnerable immatures by adults, leading to a decrease in population density. Separation of eggs and juveniles from adults could reduce the effects of limited resources and cannibalistic behaviour, however this method is labour intensive. The provision of pollen as an alternative food source has been found to increase natural enemy populations, and in some instances, prevent cannibalistic behaviour (Castagnoli *et al*. 1999; Samaras *et al*. 2015; Vangansbeke *et al*. 2014b). However, this was contrasted by a study conducted by Vangansbeke *et al.* (2014a), where female *A. limonicus* tended to consume their own eggs when fed on a pollen diet.

Increasing the habitat complexity in a mass rearing system may be a simple and effective solution to overcrowding. While, increasing spatial complexity has not been shown to directly decrease cannibalism, it can benefit natural enemy populations (Faraji *et al*. 2002; Ferreira *et al*. 2008; Roda *et al*. 2000). This is because complex structured habitats can provide refuge, oviposition sites, and create a more favourable microclimate (Ferreira *et al*. 2008; Janssen *et al*. 2007; Langellotto & Denno 2004; Roda *et al*. 2000). Rickers and Scheu (2005) demonstrated that juveniles were frequently preyed upon in a treatment with a simple habitat structure. Whereas in a complex habitat, juveniles were able to gain refuge from cannibalistic adults leading to a lower mortality rate.

This study investigated how rearing media could be utilised to increase the spatial complexity of a habitat, and thereby increase predator populations through a reduction of cannibalism. Five different rearing media were used to create microenvironments in a closed system with pollen and water supplementation. The materials chosen were buckwheat husks, gorse husks, rice husks, vermiculite, and wheat bran. These were compared to a control treatment with no substrate. In addition, these treatments were tested at two different humidities to assess any differential population effects on *A. limonicus*. The addition of materials was predicted to increase predator populations as eggs and juveniles seek refuge in the structurally complex habitats.

Methods

Mite Colony

Amblydromalus limonicus individuals were initially obtained from black nightshade (*Solanum nigrum* Linnaeus) in St Johns, Auckland. Mites were reared on *Typha orientalis* (Presl) pollen that is similar to the pollen of the closely related *T. latifolia* species (Linnaeus) which produces the highest intrinsic rates of increase compared to other species (Samaras *et al*. 2015). The pollen used for the colonies and experiments was collected from the St Johns district in the summer of 2014. It was subsequently air dried using an oven at 30ºC and stored in a -18ºC freezer. Mite colonies were maintained on laboratory rearing trays at Landcare Research, Auckland, New Zealand.

Rearing trays consisted of circular black plastic arenas (14.5 cm diameter) placed on an inverted petri dish which were wrapped with three paper towels (Figure 1). Two rubber bands were used to fix the petri dish to the plastic arena. This was then placed in a plastic tray containing distilled water to ensure that the tissue would remain wet and thus provide water access to the mites via the periphery of the petri dish. Long pieces of thread were distributed across the tray to provide additional sites for refuge and oviposition. Pollen was provided by putting ten 3 cm strips of cotton thread into a plastic vial containing pollen and shaken vigorously (Adar *et al*. 2014). Excess pollen was then gently shaken off and the threads were spread around the plastic arena. The trays were then placed in a room with 12: 12 h (L:D) photoperiod at 25 ± 1°C in 80% relative humidity. Pollen and water were supplemented every fifth day. Multiple trays were set up in order to maintain a large number of *A. limonicus.*

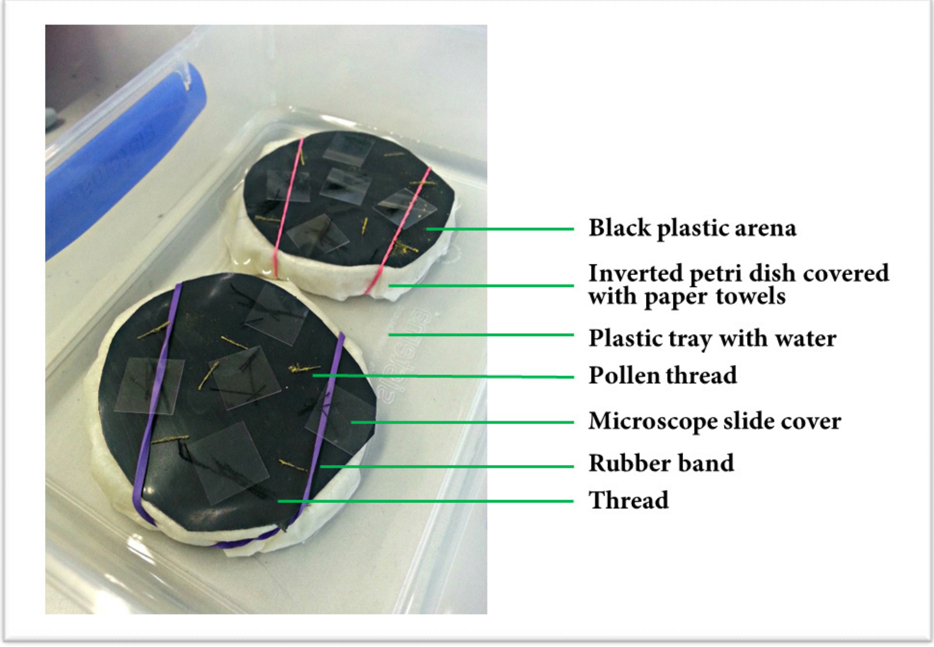

FIGURE 1. Rearing trays which were used to isolate even aged *Amblydromalus limonicus* adults. These were placed in an 85% humidity controlled cabinet at 25ºC. Photo by Ming Lee.

Rearing of even aged adult mites for experiments

Even aged adult mites were needed for experiments to ensure that the mites used in each treatment were equally fecund. To do this, 160 female *A. limonicus* were collected from the colony and placed into four separate smaller rearing trays (8.5 cm diameter) of similar design (Figure 1). Bunches of five 1 cm threads were spread around the arena with a microscope slide cover placed over each grouping. This method created a microspace for the predatory mites and also allowed for easier collection of eggs which were usually oviposited onto the thread. Separate pollen coated threads were then spread around the rearing tray. These trays were placed into the temperature and humidity controlled cabinet that had the same settings as the original mite colony. Eggs that only differed in age by one day were collected on day 2 and day 3 and placed on four separate trays to obtain similar aged mites. Adult mites which were three-four days old were used to increase the chances of successful mating and oviposition.

Effect of different rearing media on predator cannibalism

The effect of different rearing media was tested in two humidity cabinets set at 70% and 85% in a 25°C temperature controlled room. After preliminary testing, the five materials chosen were buckwheat husk, gorse seed husk, rice husk, medium sized vermiculite and wheat bran (Figure 2).

FIGURE 2. The different substrates used to increase the habitat spatial complexity for *Amblydromalus limonicus*. The following rearing substrates are shown: (a) buckwheat husk, (b) gorse husk, (c, d) rice husk, (e) vermiculite, and (f) wheat bran. Photos by Birgit Rhode.

To prepare for sterilisation, a glass vial with two 1cm strands of thread, four 1 cm glass water straws (1.5cm diameter), and 0.1g of the selected material was assembled for all replicates within each treatment (Figure 3). A control treatment with the threads and water straws was also included yielding six different treatments at each of the two humidity levels. The glass vials were then topped with cotton wool and put in an autoclave to sterilise before the experiment commenced.

After sterilisation, circular pieces of parafilm were placed on top of the rearing media to reduce the growth of mould by limiting the spread of pollen throughout the vial (Figure 3). This parafilm did not enclose mites to the bottom of the vial but was used to separate the pollen threads from the rearing media. The pieces of thread were then coated with pollen, while the glass straws were filled with distilled water using a syringe. Four impregnated females and one adult male were placed in each glass vial for each treatment. The adult male was included to increase the chances of successful reproduction (Vangansbeke *et al*. 2014b). A fine black mesh was placed at the open end of the vial and secured using a plastic lid with a hole drilled through. This arrangement allowed for respiration to occur while preventing mites from escaping. Due to limited space and time, the experiments were conducted in block trials. Two-four replicates of each treatment for both 75% and 85% relative humidity were completed within one block. A total of four separate blocks were completed which yielded between 11 to 13 replicates for each rearing media treatment in each humidity regime. The number of replicates was uneven due to complications with mould growth.

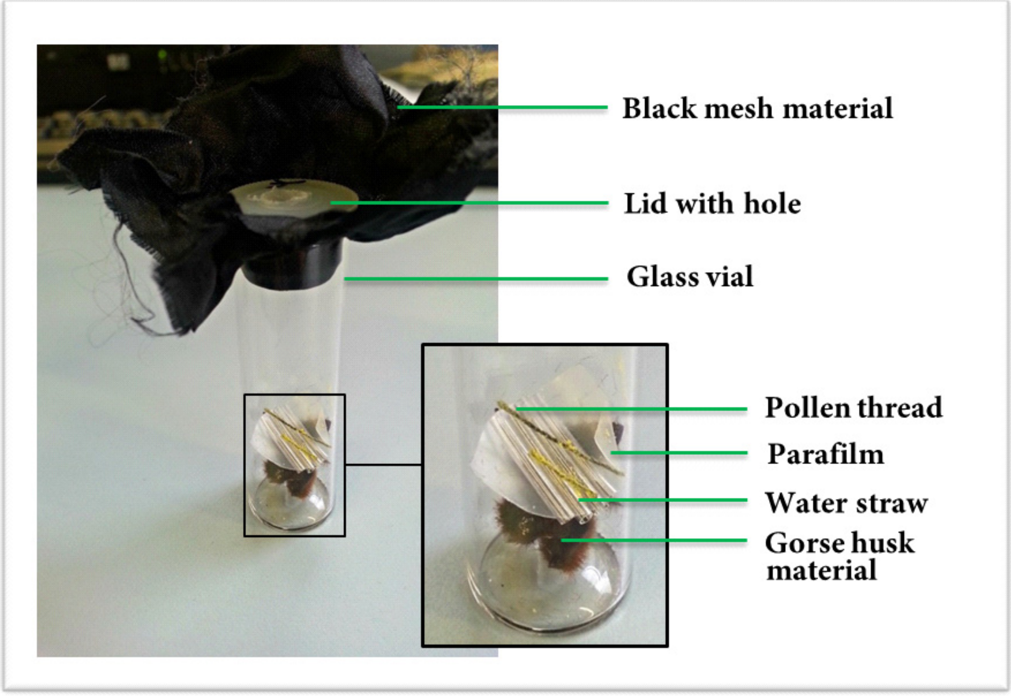

FIGURE 3. A glass vial showing the details of the environment created to test different media on cannibalism rates of *Amblydromalus limonicus* at 25ºC in two different humidity's (70% and 85%). This example uses gorse husks as the rearing media. Photo by Ming Lee.

Every two days (from days 2–12) a ten minute count of the number of eggs, larvae, nymphs and adults were recorded for each glass vial. The materials, threads, parafilm, and straws were all examined in the count. To ensure that there was a continuous supply of food and water, two freshly coated pollen threads and four water straws were added in each glass vial every four days. Each experiment ran for 14 days and was terminated by placing 90% ethanol into the glass vial. For each vial, *A. limonicus* were separated from the materials and the number of eggs, larvae, protonymphs, deutonymphs, and adults were recorded which represented the final count of the population in each glass vial. These were then placed on microscope slides with 70% lactic acid and examined under a compound microscope (Leica DM4500B) to determine their life stage and sex. This destructive sampling on day 14 allowed for accurate population counts.

Statistical analysis

One control treatment that had 35 eggs and a total of more than 80 mites was regarded as an outlier and removed from all analyses. As some of the individual life stages had very scattered data that violated the variance assumptions, a repeated measures ANOVA was only applied for the total counts from day 2 to day 12, using rearing media and humidity as factors. Additionally, a multistrata ANOVA was then conducted on the total counts for each sample period (day 2–day 12) for both materials and humidity. Further pairwise *t*-tests were used for the different materials and humidities for sample days that were shown to be significant. Similarly, another multistrata ANOVA was used to analyse each life stage of the predatory mite for the final counts (day 14). Due to low counts of protonymphs and deutonymphs, their final count was pooled together to create a new variable labelled "nymphs". Further pairwise comparisons were conducted for results that were shown to be significant. Log transformations were used for any data that violated normality assumptions (+1 was added to all y values to eliminate zeros). As the replicates were conducted in a block form, any differences between each block trial were accounted for in all analyses. All statistical analyses were done using the R Foundation for Statistical Computing package (version 3.3.1).

Results

Final population count (Day 14)

There were differences (p=0.0001) between rearing media for the final population of eggs, adults, and the total of all life stages of *Amblydromalus limonicus* (Table 1). However, there was no evidence against the null hypothesis that the final sum population of *A. limonicus* was the same for both humidities. This data contrasts the sampling data that suggests there was a relative humidity effect on the total number of predators (Tables 1, 3). There was also no evidence that suggested the rearing media and humidity have an interaction (Table 1). This means if the materials were changed, the effect on the sum population would be the same for both humidities and vice versa.

TABLE 1. Effect of rearing media and relative humidity (RH) on the populations of different life stages of *Amblydromalus limonicus.* Shown are the results from a multistrata ANOVA model done on the final count of individuals of each life stage after 14 days in a closed system. *F* refers to the F statistic produced from each ANOVA test. The degrees of freedom across all life stages for rearing media, RH, and rearing media x RH was 5, 1, 5 respectively.

Source of variation	Life stage									
	Egg		Larva		Nymph		Adult		Total	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Rearing media	4.44	**0.0009**	0.98	0.434	1.22	0.306	6.80	**<0.0001**	5.72	**0.0001**
RH	4.21	**0.042**	0.06	0.806	26.74	**<0.0001**	0.11	0.743	0.017	0.897
Rearing media x RH	1.53	0.185	1.44	0.215	2.402	**0.041**	1.75	0.128	1.24	0.296

P-values shown in bold are significant at the 0.05 level.

The final counts (day 14) revealed that rice husk had the highest total populations, while the control and wheat bran had the lowest (Table 2). Moreover, rice husk was found to have the highest population of each of the four separate life stages. However, for larvae and nymphs this was not significant (Table 2). Populations in the rice husk treatment were 59% higher than the control, whereas buckwheat and gorse husk performed 25–30% better than the control treatment.

TABLE 2. The mean ± standard error of the final counts (day 14) of each life stage which combined the data from 70% and 85% relative humidity treatments. The total shows the sum of all life stages for each rearing substrate.

Rearing media	Life stage				
	Egg	Larva	Nymph	Adult	Total
Buckwheat Husk	9.17 ± 1.40 ab	2.87 ± 0.83 a	2.22 ± 0.58 a	9.83 ± 0.82 ab	24.09 ± 2.32 ab
Control	7.86 ± 2.28 c	2.77 ± 0.91 a	1.86 ± 0.42 a	5.96 ± 1.16 c	18.45 ± 4.09 c
Gorse Husk	8.04 ± 1.33 b	2.96 ± 0.87 a	1.68 ± 0.38 a	10.36 ± 0.97 a	23.04 ± 2.11 be
Rice Husk	11.71 ± 1.21 a	3.58 ± 0.83 a	3.04 ± 0.67 a	10.92 ± 1.12 a	29.25 ± 2.04 a
Vermiculite	7.54 ± 0.99 b	2.67 ± 0.56 a	1.83 ± 0.39 a	7.75 ± 0.92 bd	19.79 ± 1.85 bc
Wheat Bran	7.24 ± 0.84 b	1.28 ± 0.38 a	2.00 ± 0.48 a	6.28 ± 0.75 cd	16.79 ± 1.31 cde

Means within each column are significantly different if they are not followed by the same letter ($p < 0.05$). Columns with all the same letters were not significant, so multiple comparisons tests were not done.

Population trends revealed by sampling (Day 2–12)

Populations were significantly affected by the rearing media, humidity, and sampling day across the monitoring period ($p<0.0001$). However, there was no significant interaction between rearing media and humidity (Table 3). Higher populations were observed in the 85% humidity treatment during monitoring, and this humidity effect was highly significant on all days except day 12 (Figures 4, 5; Table 4). The rearing media was also found to be very significant for the total populations across each sampling day (Table 4).

TABLE 3. Effect of different rearing media and relative humidity (RH) on the total populations of *Amblydromalus limonicus*. Shown are the results from a Repeated Measures ANOVA model done for the total populations across 12 sampling days. *F* refers to the F statistic produced from each ANOVA test.

Source of variation	*df*	*F*	*P*
Rearing media	5	6.94	<0.0001
RH	1	65.50	<0.0001
Day	5	52.19	<0.0001
Rearing media x RH	5	0.75	0.59
Rearing media x Day	25	4.96	<0.0001
RH x Day	5	12.25	<0.0001
Rearing media x RH x Day	25	1.70	0.02

TABLE 4. Effect of the rearing media and relative humidity (RH) on populations of *Amblydromalus limonicus* assessed on six occasions. Shown are the results from a multistrata ANOVA model conducted on the total individuals found on each sample day. *F* refers to the F statistic produced from each ANOVA test.

Source of variation	*df*	*F*	*P*
Day 2			
Rearing media	5	23	<0.0001
RH	1	10.26	0.002
Rearing media x RH	5	2.63	0.027
Day 4			
Rearing media	5	6.26	<0.0001
RH	1	78.02	<0.0001
Rearing media x RH	5	1.23	0.297
Day 6			
Rearing media	5	1.85	0.0368
RH	1	30.57	<0.0001
Rearing media x RH	5	0.4	0.714
Day 8			
Rearing media	5	4.56	0.0007
RH	1	60.77	<0.0001
Rearing media x RH	5	1.56	0.175
Day 10			
Rearing Media	5	6.25	<0.0001
RH	1	22.46	<0.0001
Rearing media x RH	5	1.74	0.131
Day 12			
Rearing media	5	5.01	0.0003
RH	1	3.16	0.078
Rearing media x RH	5	3.11	0.011

In the 70% humidity treatment, the highest populations reached were on day 6 with a slight decrease in populations thereafter (Figure 4). This effect was greater in the 85% humidity treatment and suggests the co-occurrence of two different generations (Figures 5, 6; Table 6). Buckwheat husk and gorse husk had the highest total population across the different days for both humidities, while wheat bran had the lowest populations at 70% humidity and the control treatment for 85% humidity (Figure 6). When the totals for treatments at both humidity regimes were averaged, a similar population pattern across the materials was also observed (Table 5).

Discussion

This study utilised an array of different rearing substrates in an attempt to increase habitat spatial structure and hence reduce cannibalistic behaviour. Both the sampling data and final counts revealed that the use of different rearing media had a strong effect on the population of *Amblydromalus* *limonicus*. Additionally, the bar graphs for each rearing media describe the different stage distribution patterns across the 12 sampling days for both humidities. This system revealed that there were at least two different generations co-occurring simultaneously, with the progression of egg to adulthood being achieved at approximately day 8 of the experiment.

Additionally, it highlights that the highest populations reached was between day 6 and day 8 which suggests that at these points, the populations were at the threshold limit where limitations of food and space arise. The decrease in populations thereafter can be linked to the onset of cannibalistic behaviour. Although, a profusion of fresh pollen was supplied every four days, the quality of the initial pollen strands, which typically remains fresh for one week, grew mould quickly due to the humid conditions (Nomikou *et al*. 2002; van Rijn *et al*. 2002). This meant that when individuals needed to feed, they were likely to encounter other foraging predators as they were all restricted to the fresh pollen. As mould growth was exasperated with time, overcrowding at the fresh food source was commonly observed which consequently led to a reduction of *A. limonicus* populations.

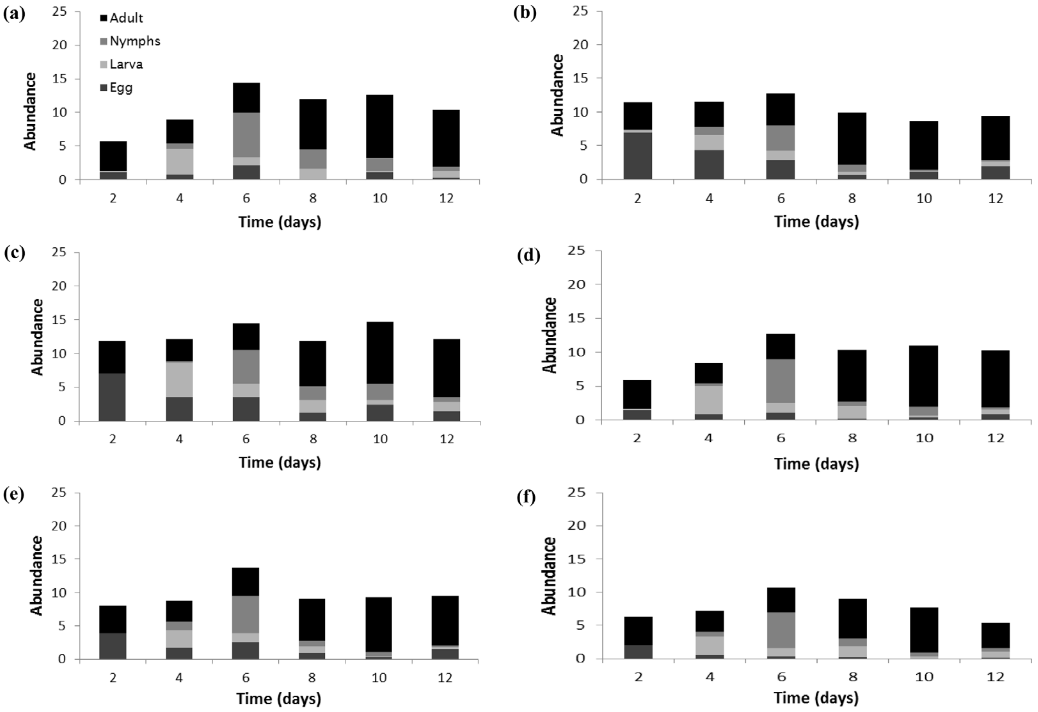

FIGURE 4. The populations of *Amblydromalus limonicus* in glass vials with (a) buckwheat, (b) no added media (control), (c) gorse, (d) rice, (e) vermiculite, or (f) wheat bran, set at 25ºC and 70% relative humidity. Different shades represent different life stages, with the entire bar representing the total of all life stages. Standard errors for each life stage could not be shown.

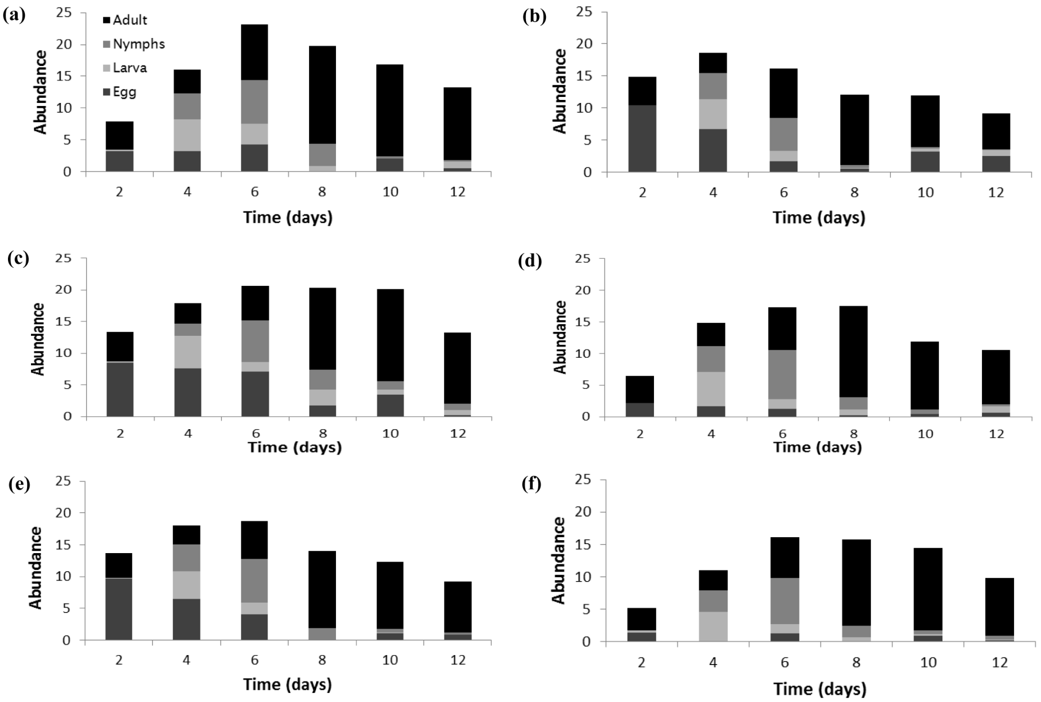

FIGURE 5. The populations of *Amblydromalus limonicus* in glass vials with (a) buckwheat, (b) no added media (control), (c) gorse, (d) rice, (e) vermiculite, or (f) wheat bran, set at 25ºC and 85% relative humidity. Different shades represent different life stages, with the entire bar representing the total of all life stages. Standard errors for each life stage could not be shown.

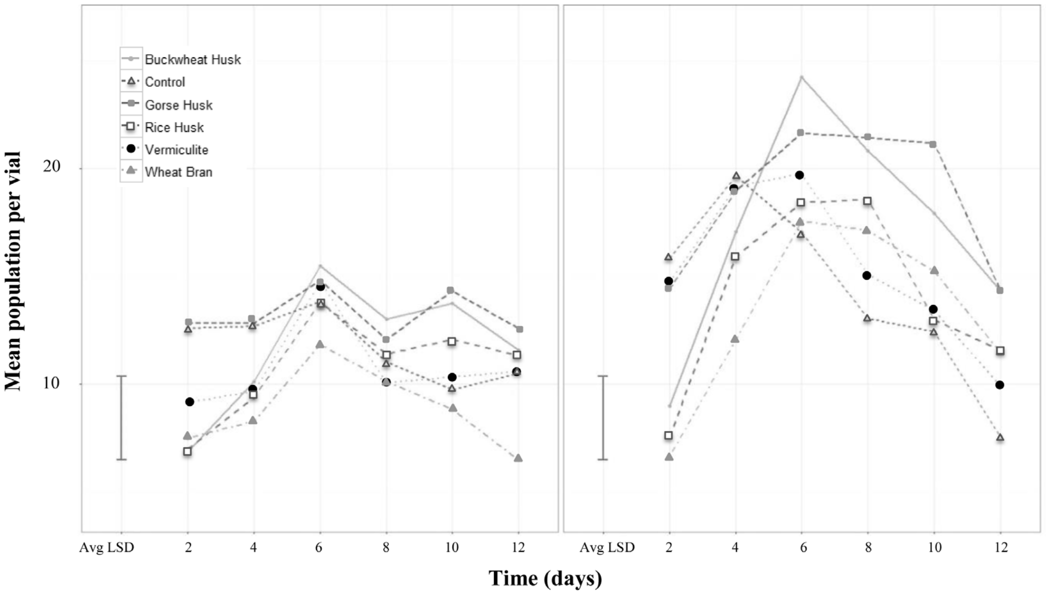

FIGURE 6. The average mean of all life stages of *Amblydromalus limonicus* in vials with six different rearing media treatments in 70% (left) and 85% (right) relative humidity. This experiment was conducted at 25ºC where the population was monitored every two days.

TABLE 5. The mean ± standard error of *Amblydromalus limonicus* populations for six rearing media per day using the combined data from experiments at 70% and 85% relative humidity.

Rearing media	Day					
	Day 2	Day 4	Day 6	Day 8	Day 10	Day 12
Buckwheat Husk	6.87 ± 0.49 bd	12.65 ± 1.18 ab	18.96 ± 1.84 a	16.00 ± 1.22 a	14.83 ± 0.78 a	11.91 ± 0.87 a
Control	13.00 ± 0.95 a	14.86 ± 1.27 a	14.24 ± 1.06 b	10.86 ± 0.83 b	9.91 ± 1.14 b	7.95 ± 0.83 b
Gorse Husk	12.60 ± 0.85 a	14.96 ± 1.27 a	17.32 ± 1.44 ab	15.88 ± 1.64 a	16.84 ± 1.69 a	12.44 ± 0.93 a
Rice Husk	6.21 ± 0.45 b	11.58 ± 0.94 b	15.04 ± 1.07 b	13.92 ± 1.33 ac	11.46 ± 0.95 b	10.38 ± 0.94 ac
Vermiculite	10.88 ± 1.06 c	13.33 ± 1.36 ab	16.17 ± 1.39 ab	11.50 ± 0.86 bc	10.79 ± 0.77 b	9.17 ± 1.03 bc
Wheat Bran	5.78 ± 0.72 bd	9.00 ± 0.82 c	13.57 ± 1.39 b	12.52 ± 1.22 bc	10.91 ± 1.10 b	7.83 ± 1.18 b

Means within each column are significantly different if they are not followed by the same letter ($p < 0.05$).

TABLE 6. The mean ± standard error of *Amblydromalus limonicus* populations at 70% and 85% relative humidity (RH) per sampling day using the combined data from six different rearing media treatments.

RH	Day					
	Day 2	Day 4	Day 6	Day 8	Day 10	Day 12
70	8.23 ± 0.51 a	9.41 ± 0.53 a	13.01 ± 0.70 a	10.19 ± 0.46 a	10.45 ± 0.54 a	9.45 ± 0.55 a
85	10.15 ± 0.61 b	15.96 ± 0.63 b	18.75 ± 0.80 b	16.73 ± 0.76 b	14.56 ± 0.77 b	10.55 ± 0.62 a

Means within each column are significantly different if they are not followed by the same letter ($p < 0.05$).

Differential performance of each substrate type

The highest total populations were when rice husks were incorporated into the closed system. This husk was found to have the highest mean population for each of the four separate life stages in the final counts. However, this effect was not significant for the larval and nymphal stages. The different range of husks provided additional space for the predatory mites to shelter and oviposit in, however rice husks have a narrower opening compared to other husks which may have been more capable in enclosing the predatory mites (Figure 2). Furthermore, as weight was used to control the amount of substrate used, a larger number of individual rice husks was obtained which created more space compared to the other denser materials. Wheat bran, followed by the control, performed the worst in regards to reducing cannibalistic behaviour. This pattern was consistent with the sampling data and is similar to what was hypothesised. In the control treatment, the predatory mites were exposed with little to no refuge and were thus extremely vulnerable to predation (Rickers & Scheu 2005). In addition, gravid females tended to lay their eggs on pollen threads where populations would gather to feed. This meant that as eggs hatched, the emerging larvae were confronted with a foraging predator, which thereby increased the likelihood of cannibalism. This thus contributes to the lower population of *A. limonicus* in the control treatment. As the wheat bran treatment was severely affected by mould, it in effect was not a good representation of how rearing media can be used to increase habitat spatial complexity. Consequently, excluding wheat bran, all treatments which included some form of rearing substrate, performed better than the control treatment. However, this difference was not significant for the vermiculite treatment.

Effects of habitat complexity on predator populations

Increasing the habitat spatial complexity of a system has a range of effects on community dynamics and various hypotheses have emerged to explain why natural enemies congregate in these habitats. The most prevalent propositions suggest that structurally complex habitats may reduce encounter rates, provide refuge from predation, and create a more favourable climate (Janssen *et al*. 2007; Langellotto & Denno 2004; Roda *et al*. 2000). This consequently reduces predation rate and thus a greater population is achieved. For example, a meta-analysis that assessed the effect of habitat structure on 62 independent taxa that included hemipterans, mites, spiders, and parasitoids, showed that an increase in habitat spatial complexity resulted in significant increases in natural enemy abundance, while a decrease significantly diminished populations (Langellotto & Denno 2004). Benefits of habitat structure are not limited to the Arthropoda phylum as an increase in habitat heterogeneity has been linked to better community stability, a lower predation risk, and an increase in species diversity for bivalves, fish, and avian species (Gorman & Karr 1978; Heck & Crowder 1991; Irlandi 1994; Whittingham & Evans 2004).

The higher populations found in the current study coincides with the findings of Halaj *et al.* (2000), where the habitat within soybean fields were manipulated to produce a habitat refugia for generalist predators. They found that there was 60% more spider species where a habitat refuge was present compared to the open field, with further significant increases in the abundance of harvestmen and predatory beetles. The proportion of spiderlings and egg sacs were also higher in the treatment with habitat refugia which was linked to increases in spider reproduction. The current study also found a higher abundance of eggs, larva and nymphal stages in three treatments that contained rearing substrates compared to the control. However, for the immature stages this effect was not significant.

By introducing materials into an enclosed area, it increased the spatial structure of the environment which likely explains the discrepancy observed between the treatments with substrate as opposed to no substrate. Eggs were frequently found on the inside of buckwheat husks and rice husks, while for gorse, eggs were laid on the outside where an abundance of fine hair fibres were present. The preference of reproductive females for structurally complex habitats may reflect more suitable climatic conditions present for egg development (Halaj *et al*. 2000). This is particularly important as eggs of *A. limonicus* are particularly sensitive to low relative humidity with no eggs hatching at 50% or lower and only 50% hatching at 60% humidity (McMurtry & Scriven 1965).

Discrepancies between final counts (day 14) and sampling data (day2–12)

The monitoring data indicates that there was a significant difference between the two humidities in the total populations for all sample days, with the exception of day 12. This reflects the expected result as *A. limonicus* populations were predicted to be lower in the 75% humidity treatment and higher in the 85% humidity treatment due to their preference for high humidity conditions (McMurtry & Scriven 1965). However, this is contrasted by the more accurate final sum count (day 14) which revealed that there was in fact no significant difference in the population of *A. limonicus* between the two different humidities. This absence of the humidity effect may have been moderated to some extent by the addition of the water straws and materials. The open nature of the water straws meant that for both treatments, a higher humidity was present within each vial than was recorded. In addition, treatments with rearing media may act similar to leaf surface structures and further increase the availability of higher humidity environments (Roda *et al*. 2000). This means that in the low humidity treatment, *A. limonicus* may have utilised the surrounding substrate more frequently due to its ability to provide a more favourable microclimate. While for the higher humidity treatment, the rearing media may have been employed less due to already favourable conditions. This behaviour would have incontrovertibly decreased their detectability in the 75% RH treatment, which fundamentally resulted in these samples deviating further from the actual number of the predators. While for the 85% RH treatment, the predatory mites would have been easier to discern due to their decreased need to reside within the rearing media leading to a higher count. These observed differences ultimately contributed to a false humidity effect in the sampling data.

The monitoring data contrasts the final counts in classifying which rearing media produced the highest mite populations. For both the 70% and 85% humidity treatments, the monitoring data reveals that buckwheat husk and gorse husk had the highest populations during the last count. This discrepancy between the final sum count and monitoring count largely stems as a result of sampling bias. Although, the duration of monitoring was kept constant across all replicates, the properties of the substrate did affect sampling accuracy. For example, in the rice husk treatment, predators were able to hide within the husks obscuring their ability for detection, while for the control treatment, a more accurate sample of the population was taken as there were fewer objects obscuring their observation. This also explains the unexpected result of a rearing media effect on day 2 and day 4 of sampling. Although, the total number of the predators was similar at the beginning of the experiment, the differences in detectability produced a highly significant substrate effect at the onset of the experimental period. The detectability of predatory mites in the rice husk and wheat bran treatments was particularly difficult as mites were relatively well camouflaged and able to hide in the many available crevices. There was thus a tendency to undersample in treatments where the rearing media were able to effectively shield away *A. limonicus.* However, for wheat bran, the heavy growth of mould in the later stages reduced sampling bias as mites were forced up towards the top of the glass vials allowing for a more accurate count.

Relationship between substrates and mould growth

The low populations of the predatory mite in wheat bran are likely the result of mould growth rather than the effect of cannibalism. Although all materials that could be sterilised were done so, the growth of mould was apparent in all treatments due to the relatively humid experimental conditions. Like most fungi, the growth of mould is proliferated in an environment where high moisture exists (Galloway 1935; Grant *et al*. 1989; Ryu & Moon 2014). This was emphasised in treatments that had rearing substrates that were particularly hygroscopic.

Wheat bran is categorised as highly hygroscopic and evidence of mould was usually seen by day 4 of sampling, with heavy infestations seen by day 6 in some instances (Nagi *et al*. 2012; Roozendaal *et al*. 2012). Though rice husk is also classified as hygroscopic, the husk largely acts as a barrier in the rapid water absorption process for the rice grain and this is reflected in the samples where the growth of mould was largely impeded (Indudhara *et al*. 1971; Thakur & Gupta 2006). Similarly, while vermiculite is also a hydrous material, this treatment had correspondingly low rates of mould infestation compared to wheat bran (Aristov *et al*. 2000). As most mould fungi obtain nutrients through organic substances, the magnesium-aluminium silicate material that vermiculite is composed of is not an ideal host, resulting in reduced mould growth (Erkmen & Bozoglu 2016). However, mould is still present within this treatment due to the organic pollen present in each vial. Buckwheat treatments also had relatively low levels of infestation and this may be due to the media having been heat treated which eliminated some of its moisture content. Treatments that included gorse husk had a relatively high severity of mould infestation, however, there is no literature surrounding its moisture absorption properties. If a method was developed that would reduce mould growth significantly, gorse husk should be reconsidered as an effective rearing media as gravid females highly favoured ovipositing on the villous seed pods as opposed to the cotton thread. Immatures were also observed to reside within these dense mats of hair which reduced the speed in which the predators were able to navigate in. However, a limitation of this substrate is that this material cannot be easily collected or purchased at a global scale.

As the growth of mould is inconsistent between different rearing substrates, this infestation has been a confounding factor in determining the ability of a rearing media to reduce the cannibalism rate of *A. limonicus*. A possible way to improve this experimental design may be to substitute a modified leaf disc system instead of using glass vials. In this way, the water straws would not be required and the effect of mould would be reduced. Considering that the application of these materials would be utilised in environments with high moisture and/or humidity, it is important to include the effect of mould infestation when establishing the success of each material.

Substrates in wider applications and research recommendations

The ability of rearing media to increase habitat spatial complexity and hence reduce cannibalism can be hugely beneficial for mass rearing practices. Substrates that substantially increase the population output of natural enemies without the addition of expensive equipment will greatly enhance the cost effectiveness of mass rearing. Depending on the facilities and methods used in commercial mass rearing, rice husks may be easily incorporated into the rearing system by simply spreading across trays or by placing the substrate within a bag on rearing trays. Rice husks should also be considered for the transportation and application procedures in the horticultural setting. Vermiculite is the most commonly utilised substrate for these processes which has now been revealed to underperform compared to other rearing media (Colfer *et al*. 2004; Lesna *et al*. 1996; Navarro-Campos *et al*. 2016; Shaw & Wallis 2007). In addition, rice husk is regarded as a waste material and can be obtained very inexpensively which would reduce the operational costs of biological control operations.

Future research should focus on the behavioural aspects of cannibalism in *A. limonicus* as many parameters are still not well understood. For example, when there was an abundance of food and limited numbers of predators, cannibalism was still observed. In this scenario, cannibalism may have been an interaction that was applied to reduce population size before acute resource shortages occur. Further understanding of this prevalent phenomenon will be exceedingly beneficial to the application of *A. limonicus* and other cannibalistic predators for mass rearing and biological control operations.

Conclusion

By gaining a better knowledge of how specific structural elements may moderate antagonistic interactions between predators, larger populations of natural enemies can be achieved. Increasing the spatial complexity of the microenvironment in which predatory mites interact was shown to be a solution to overcrowding. For *A. limonicus*, rice husk was the most suitable rearing media because it was the least susceptible to mould growth, and provided additional shelter and oviposition sites. This resulted in the highest populations of *A. limonicus* compared to other substrate treatments. Rice husk proves to be a great candidate to improve current mass rearing methods of *A. limonicus* and should also be considered for other phytoseiid biological control agents.

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